Running head: PERIPHERAL RESPONSES TO ANGRY PROSODY

Peripheral Responses to Attended and Unattended Angry Prosody:

A Dichotic Listening Paradigm

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Abstract

We investigated the effects of angry prosody, varying focus of attention, and laterality of presentation of angry prosody on peripheral nervous system activity. Participants paid attention to either their left or their right ear while performing a sex discrimination task on dichotically presented pseudo-words. These pseudo-words were characterized by either angry or neutral prosody and presented stereophonically (anger/neutral, neutral/anger, or neutral/neutral, for the left/right ear, respectively). Reaction times and physiological responses (heart period, skin conductance, finger and forehead temperature) in this study were differentially sensitive to the effects of anger versus neutral prosody, varying focus of attention, and laterality of presentation of angry prosody.

Keywords: emotion, attention, lateralization, prosody, anger, dichotic listening, peripheral nervous system, heart period, skin conductance, forehead temperature, finger temperature

Peripheral Responses to Attended and Unattended Anger Prosody: A Dichotic Listening Paradigm

Whereas the effects of other persons' facial emotional expressions on peripheral responding have been widely studied (e.g., Dimberg & Petterson, 2000), research investigating the effects of other persons' vocal emotional expressions on peripheral responding has remained remarkably sparse (e.g., Mitchell, 2006). This is surprising because emotional prosody, defined as supra-segmental and segmental modulations of acoustical parameters of speech related to emotional processes (Grandjean, Bänziger, & Scherer, 2006), plays a critical role in everyday life (Russell, Bachorowski, & Fernandez-Dols, 2003; Scherer, 1986, 2003). Moreover, several disorders such as schizophrenia and autism have been related to impaired perception and expression of emotional prosody (e.g., Bach et al., 2009; Hoekert, Kahn, Pijnenborg, & Aleman, 2007; Peppé, McCann, Gibbon, O'Hare, & Rutherford, 2007), emphasizing its importance for social interactions.

The study of angry prosody is of particular importance because angry prosody signals potential danger for individual well-being, even if face-to-face contact is prohibited. Orientation, rapid physiological adaptation, and response preparation for such threatening social situations have been prerequisites for survival and social adaptation, both phylogenetically and ontogenetically (Öhman & Wiens, 2003; Panksepp, 1982; Plutchik, 1980). In threatening situations, it can be essential to automatically orient and prepare physiological responses that support the accomplishment of adaptive behavioral actions even if, or especially when, voluntary attention is initially devoted to something else. Emotional stimulus material in the visual domain has been shown to capture attention (e.g., Bradley & Lang, 2000; Lipp & Waters, 2007; see Vuilleumier, 2005, for a review)—with and without the involvement of conscious or voluntary processes—and to initiate remarkable mobilization for action preparation (Öhman & Mineka, 2001). For example, Öhman, Esteves, and Soares (1995) demonstrated elevated electrodermal activity to reflect the preattentive processing of masked fear-conditioned faces. For the auditory domain, Grandjean, Sander, Lucas, Scherer, & Vuilleumier (2008) found that auditory extinction in right-hemisphere patients with left spatial neglect syndrome can be reduced when contralesional auditory stimuli are emotionally significant. Thus, emotional stimuli have been successfully demonstrated to capture attention (exogenous attention).

In turn, the deployment of voluntary (or endogenous) attention has been repeatedly shown to modulate central nervous system activity during the processing of emotional facial expressions (e.g., Holmes, Vuilleumier, & Eimer, 2003; Pourtois, Grandjean, Sander, & Vuilleumier , 2004; Vuilleumier, Armony, Driver, & Dolan, 2001). However, few studies have explicitly examined the combined effects of voluntary attention and emotion in the auditory domain (e.g., Grandjean et al., 2005, Sander et al., 2005; Schirmer, Kotz, & Friederici, 2005). Moreover, to the best of our knowledge, no single study has investigated the effects of these manipulations on peripheral nervous system activity.

Grandjean and collaborators (2005; see also Sander et al., 2005) investigated the neural correlates of attended versus unattended angry prosody in a dichotic listening paradigm. In this study, male and female voices were presented to the left and right ears of participants. These voice stimuli were characterized by either angry prosody or neutral prosody and presented stereophonically (anger/neutral, neutral/anger, or neutral/neutral, for the left/right ear, respectively). Participants were instructed to attend to either their left or their right ear and to denominate the sex of the voice presented to the attended ear. Thus, emotional prosody was not explicitly judged in the task to be performed (sex discrimination task). Voice-selective areas in both hemispheres (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000), especially the bilateral superior temporal sulcus and the right amygdala, displayed greater activation for angry as compared with neutral prosody, irrespective of whether the ear receiving the angry prosody was attended to or not. Such an observation suggests once more that significant signals such as angry prosody can capture and direct attention. Furthermore, the medial portion of the orbitofrontal cortex, the cuneus in the medial occipital cortex, and the bilateral ventrolateral prefrontal cortex displayed greater activation when angry voice prosody was presented to the attended ear than when it was presented to the unattended ear (Sander et al., 2005; cf. data from the facial domain: Pourtois et al., 2004; Vuilleumier, 2002). Together, these results favor a model of multiple levels of processing of angry prosody, with areas sensitive to voluntary attention (as compared with areas insensitive to voluntary attention) reflecting more integrative stages of affective evaluation.

Reaction times in Grandjean et al.’s (2005) and Sander et al.’s (2005) sex discrimination task were slowed when an angry voice was presented to the left ear, but only when this ear had to be attended. The authors interpreted this as a sign for the superiority of the left ear/right hemisphere for the processing of auditory emotional stimuli (cf. Borod & Madigan, 2000; Jäncke, Buchanan, Lutz, & Shah, 2001), allows the processing of emotional prosody even if prosody is task irrelevant. In the literature, right-hemisphere superiority has repeatedly been reported for the processing of facial emotional expressions and also for prosodic emotional expressions (Dimberg & Petterson, 2000; Kucharska-Pietura, Phillips, Gernand, & David, 2003; Ross, Edmondson, Seibert, & Homan, 1988). Rodway and Schepman (2007) observed a right-hemisphere advantage for genuine emotional prosody (cf. Herrero & Hillix, 1990; Ley & Bryden, 1982; Schmitt, Hartje, & Willmes, 1997), but not for morphed emotional prosody (fundamental frequency of emotional utterances taken and imposed on initially neutral utterances) in a dichotic listening paradigm. They concluded that the “laterality effect may be a useful tool for the detection of fake emotions” (p. 31). Thus, for angry prosody processing, the right hemisphere might play a pivotal role in the detection of real threat—but not necessarily a unique role. Processes related to fine temporal discrimination have been associated with the left hemisphere and are also important in emotional prosody processing (Schirmer & Kotz, 2006).

The latter example shows that the hypothesis of a right-hemisphere advantage for the processing of emotional events has not remained unchallenged. Brosch, Grandjean, Sander, & Scherer (2008) stereophonically presented utterances with angry/neutral spatially lateralized prosody (with angry prosody being presented either to the left or the right space by means of a head-related transfer function) or with neutral/neutral prosody to participants (cf. Grandjean et al., 2005) who were engaged in a visual dot probe paradigm. Shortly after the presentation of the utterances, the participants saw a dot appearing on a computer screen and had to say whether the dot had been displayed in their right or left hemifield. Because angry prosody is supposed to trigger exogenous attention, valid trials were those in which the hemifield of the dot corresponded to the hemispace in which the angry prosody had been presented. Conversely, invalid trials were those in which the presentation sides of angry prosody and the dot diverged. Brosch et al. observed a facilitation effect (mirrored in a shortening of response times) of the valid cueing by angry prosody for the right hemifield only. Therefore, these data might indicate an advantage of the left hemisphere for the processing of angry prosody. Finally, unlateralized effects can be found in the literature as well (e.g., Caltagirone et al., 1989; Ethofer, Van de Ville, Scherer, & Vuilleumier, 2009; Kotz et al., 2003; Kowner, 1995).

A prominent model in research on the hemispheric lateralization of emotion (cf. Davidson, Abercrombie, Nitschke, & Putnam, 1999; Harmon-Jones & Allen, 1998) suggests that emotions generally associated with approach tendencies, such as anger, rely on left-anterior-hemispheric processing, and emotions generally associated with withdrawal tendencies, such as fear, rely on right-anterior-hemispheric processing. Applying the model to the perception of angry prosody is, however, complicated because, depending on their own subjective coping potential and environmental standards, listeners may respond to the perceived threat by either approach *or* withdrawal tendencies. Together, the current state of research in the area demonstrates that the role of hemispheric lateralization in the processing of emotional, especially angry, prosody needs further investigation.

Because research on emotional prosody for peripheral nervous system activity is virtually nonexistent, the aims of the current study were threefold. First, we investigated the general effects of angry versus neutral prosody on peripheral responding. Second, we examined whether variations in voluntary attention modulate the effects of angry prosody on peripheral responding. Third, we investigated a potential ear/hemisphere advantage for the processing of angry prosody and whether such an advantage is also reflected in peripheral nervous system activity.

Our participants were instructed to perform a sex discrimination task for pseudo-words verbalized by male and female speakers in a dichotic listening paradigm (cf. Grandjean et al., 2005; Sander et al., 2005). The voice stimuli used in this sex discrimination task were characterized by either angry or neutral prosody and presented stereophonically (anger/neutral, neutral/anger, or neutral/neutral, for the left/right ear, respectively). Specifically, participants attended to either their left or their right ear and decided on the sex of the voice presented to the attended ear. Thus, emotional prosody was literally irrelevant to the behavior task. Heart period, mean skin conductance, forehead temperature, and finger temperature were continuously measured during the task. The following questions and derived hypotheses were investigated:

Question 1: How is angry prosody reflected in behavioral data and peripheral nervous system activity? We expected shorter reaction times in the sex discrimination task for the neutral/neutral as compared with the angry/neutral and neutral/angry prosody trials. This is because less attention should be directed to the less threatening neutral prosody. Effects of exogenous attention toward angry prosody should also be reflected in heart periods. Because bradycardia has been observed in previous studies investigating attentional processes toward threat (cf. Bradley & Lang, 2000), we expected increased heart periods for angry as compared with neutral utterances. Because both attentional processes and increased response mobilization have been linked to skin conductance (e.g., Bradley, Codispoti, Cuthbert, &

Lang, 2001; Gomez, Stahel, & Danuser, 2004), a higher mean skin conductance was predicted when participants listened to angry prosody than when they listened to neutral prosody. As a result of rudimentary body preparation for potential fight, we further anticipated heightened finger temperature in response to angry versus neutral prosody (cf. Levenson, Ekman, & Friesen, 1990). Finally, a more elevated forehead temperature was expected for angry prosody than for neutral prosody on the basis of observations made by Zajonc and collaborators (McIntosh, Zajonc, Vig, & Emerick, 1997; Zajonc, Murphy, & McIntosh, 1993) for negative subjective feeling states.

Question 2: Are the behavioral data and the peripheral efference of angry prosody modulated by the focus of voluntary attention? This question addressed whether our participants displayed particularly slow reaction times in the sex discrimination task when the ear receiving angry prosody was the focus of voluntary attention (cf. Grandjean et al., 2005; Sander et al., 2005). Similarly, we investigated whether the physiological effects of angry prosody varied as a function of focus of voluntary attention.

Question 3: Is there a right- or left-hemisphere advantage for the processing of angry prosody (i.e., is it reflected in behavior and physiological responding)? Because results in the literature are contradictory regarding a potential hemispheric advantage for the processing of angry prosody, we had no a priori hypotheses for this question.

Method

Participants

Forty-two healthy female undergraduate students at the University of Geneva, aged between 19 and 34 years (*M* = 22.7, *SD* = 3.12) and without any history of audiological illness, took part in this study. They were all right-handed and recruited in an introductory psychology course. Participants were paid 15 Swiss francs each. Exclusion criteria for participation were (a) medical treatment, (b) pregnancy, (c) drug abuse, and (d) age below 18 or above 35 years.

Stimuli

The auditory stimuli were produced by actors and taken from a database previously acquired and analyzed by Banse and Scherer (1996). We used three different tokens of nonsense syllable sequences (pseudo-words: "goster," "niuvenci," and "figotleich") extracted from meaningless sentence-like utterances. These voices were previously judged to express anger or neutral prosody, as validated in earlier behavioral studies (Banse & Scherer), showing an average accuracy of 75% for anger recognition (see also Brosch et al., 2008). Male and female speakers were equally distributed across conditions. The stimuli were matched for duration (750 ms). The mean acoustic energy was also counterbalanced across stimuli to avoid loudness effects.

Setting and Apparatus

Participants sat comfortably in a reclining position. Their arms were placed on an armrest to prevent fatigue to the largest possible extent. The pseudo-words were presented over headphones. Physiological data acquisition was performed continuously with the Biopac TEL 100 Remote Monitoring System (Santa Barbara, CA, USA). There were different settings for the electrocardiogram, temperature, and skin conductance channels (see section Dependent Variables for details). Signals were transferred from the experimental room to the MP 100 Acquisition Unit (16 bit A/D conversion) in the control room and stored on computer hard disk. A digital channel received inputs from the presentation computer and recorded on- and offset of presented pseudo-words. Experimental control, such as sound presentation and computer synchronization, was performed by e-prime 1.1. A hidden camera (Sony EVI-D31) permitted the detection of larger body movements impinging on physiological responses.

Procedure

Participants were told that they were taking part in a study examining the effects of male and female voices on physiological responding. Upon participants' arrival at the laboratory, the nature of the experiment was explained and written informed consent was obtained in accordance with the Helsinki Declaration of Human Rights (1991). After sensor placement, a 5-min relaxation period began, allowing the participants to become familiar with the experimental setting and to establish a physiological baseline.

Voluntary attention (left vs. right ear) was manipulated orthogonally to emotional prosody in a dichotic listening paradigm, in which two stimuli were simultaneously presented, one to each ear (anger/neutral [AN], neutral/anger [NA], and neutral/neutral [NN], on the left/right side). Every experimental trial consisted of one female and one male voice pronouncing the same pseudo-word. Participants were instructed to selectively attend the voice presented to either the left or the right ear and to decide on the sex of the speaker uttering the pseudo-words in the attended ear. Participants revealed their decision by pressing one of two buttons of a button box. Sex-button contingencies were counterbalanced across participants.

A total of 120 trials were presented to each participant. In one block (60 trials), the students focused on the voices presented to their right ear; in another block (60 trials), they attended to the voices presented to their left ear. The block sequence was counterbalanced across participants. The intertrial interval (ITI) was between 8 and 10 s (jittered presentation). Participants listened to the utterances (750 ms) and then gave their behavioral response while waiting for the next utterance. We chose this rather long ITI to account for the type of physiological responses investigated in this study (rather long latency signals). In a postinterview, participants were asked about their physical and psychological well-being. None of the participants reported having been disturbed. Before leaving the laboratory, participants were debriefed.

Dependent Variables

Behavioral data. Reaction times in the sex discrimination task were measured for each trial and participant.

Physiological data. The following physiological signals were recorded continuously with a sampling rate of 1000 Hz. Parameterization was performed with the program PPP 7.12 (2005; extra Quality Measurement Systems, Frankfurt am Main, Germany).

Heart period. Heart period (in seconds) was assessed by the use of Biopac pre-gelled disposable Ag/AgCl electrodes (10-mm sensor diameter). Electrodes were fixed according to Einthoven II, one below the right clavicle and another below the left lateral margin of the chest. Amplification was set to 500 and filters were set to 1 and 45 Hz.

Mean skin conductance. Electrodermal activity was measured with a constant voltage of 0.5 V, using the SS 3A Biopac electrodermal response transducer filled with Biopac GEL 101 electrode paste (formulated with 0.5% saline in a neutral base). The transducer was placed at the volar surfaces of the medial phalanges of the index and ring fingers of the left hand. Amplification was set to 500 (corresponding to a sensitivity of 20 μS/V) and filters were set to DC and 10 Hz. The signal was smoothed by a moving average (length: ± 200 ms).

Forehead and finger temperature. A Biopac temperature probe (SS 7) was fixed on the forehead to measure forehead temperature in degrees Fahrenheit. Finger temperature was measured with a Biopac fast response temperature probe (SS6) placed on the participants' little finger. Amplification was set to 500 (corresponding to a sensitivity of 10°F/V) and filters were set to DC and 10 Hz. The signal was smoothed by a moving average (length: ± 200 ms).

Physiological responses during the 2 s before voice onset served as baseline and were subtracted from responses estimated for the 5 s following the pseudo-words (for skin conductance, the interval comprising 1-7 s following stimulus onset was considered). The resultant difference scores represented the change provoked by a particular combination of pseudo-words (AN, NA, or NN).

Data Analysis

Angry versus neutral prosody. In a first step, a paired *t* test contrasting angry versus neutral prosody was calculated for each variable (one-tailed testing was due to a priori hypotheses, addressing question 1).

Effects of attention focus and presentation laterality for angry prosody. In a second step, responses to neutral prosody (NN) trials attended with the right (left) ear were subtracted from responses to angry prosody (AN and NA) trials attended with the right (left) ear to reduce global sensitivity differences between the two ears. Then, an analysis of variance (ANOVA) with the within-participants factors attention focus (voluntary attention to left versus right ear) and presentation laterality (anger presented to left versus right ear; AN versus NA) was calculated (addressing questions 2 and 3).

Reaction times, heart period, mean skin conductance, forehead temperature, and finger temperature were entered as dependent variables in all analyses.

Results

Behavioral Data

Participants displayed a high level of accuracy in the sex discrimination task ($M_{correct}$ = 90.0%). The proportion of correct responses did not vary across the experimental conditions (χ^2 = 9.23, p = .10, Wilcoxon test). Incorrect trials and outliers (deviating more than 3 standard deviations from the average individual reaction time across all experimental conditions; 2.5%) were eliminated from reaction times and substituted with a participant's average reaction time for the respective condition.

Angry versus neutral prosody. Consistent with our hypotheses, participants displayed longer reaction times for angry prosody than they did for neutral prosody, $t(41) = 2.57$, $p < .01$ (one-tailed, *M*s = 729.20 ms and 703.19 ms, respectively).

Effects of attention focus and presentation laterality for angry prosody. The ANOVA performed on reaction time data for angry prosody only (including the AN and NA presentations) failed to demonstrate a significant effect of attention focus, $F(1, 41) = 0.21$, *ns*, partial $\eta^2 = .00$, and presentation laterality, $F(1, 41) = 0.48$, *ns*, partial $\eta^2 = .01$. A trend was observed for their interaction, $F(1, 41) = 2.93$, $p = .09$, partial $\eta^2 = .07$ (Figure 1). Contrary to earlier research, confidence intervals (CIs) for the interaction showed a slowing of reaction times in the unattended anger conditions as compared with the NN condition (recall that the NN reaction times had been subtracted before entering the AN and NA trials into the ANOVA; CIs: 8.20 < AN, attention right < 61.42; 0.93 < NA, attention left < 69.53). Reaction times in the attended anger conditions were comparable to those in the NN condition (CIs: -7.29 < AN, attention left < 57.33; -23.35 < NA, attention right < 41.32).

Figure 1 about here

Physiological Data

Heart period data for one participant were excluded because of arrhythmia. In addition, trials in which there were incorrect responses in the sex discrimination task and outliers (deviating more than 3 standard deviations from the average individual response across all experimental conditions; approximately 2.8% of all responses) were removed from all physiological responses and substituted with a participant's average response for the respective condition.

Angry versus neutral prosody. Consistent with our hypotheses, angry prosody in comparison with neutral prosody was associated with a higher mean skin conductance, $t(41) = 2.68$, $p = .005$ (*M*s = 0.02 mrho and 0.01 mrho, respectively) and a higher forehead temperature, $t(41) = 2.35$, $p = .01$ (*M*s = 0.008 °F and 0.007 °F). Contrasts for heart period, $t(40) = 1.34$, *ns* (*M*s = -0.007 s and -0.009 s), and finger temperature, $t(41) = 1.16$, *ns* (*M*s = 0.004 °F and 0.002 °F), failed to reach significance.

Effects of attention focus and presentation laterality for angry prosody. Table 1 displays the results of the ANOVAs performed for the four physiological measures. Longer heart periods were observed when angry prosody was presented to the right ear than when it was presented to the left ear, irrespective of focus of attention (Figure 2). Moreover, CIs revealed that the AN trials did not significantly differ from the NN trials (which had been subtracted before entering the angry-prosody trials into the ANOVA; CI: -0.004 < AN < 0.003). By contrast, the NA trials did differ significantly from the NN trials (CI: 0.001 < NA < 0.007). Our heart period data thus are not supportive of the hypothesis of a right-hemisphere advantage for the processing of angry prosody.

Insert Table 1 and Figure 2 about here

Mean skin conductance varied as a combined function of attention focus and presentation laterality of angry prosody. Figure 2 reveals that the attended angry prosody conditions were associated with a higher mean skin conductance than were the unattended anger prosody conditions. However, only attended anger presented to the left ear was significantly different from the neutral (NN) utterances (CIs: 0.001 < AN, attention left < 0.032; -0.001 < NA, attention right < 0.024-0.006 < AN, attention right < 0.027; -0.009 < NA, attention left < 0.015).

The marginally significant main effect of presentation laterality for finger temperature was qualified by the significant interaction of Attention Focus × Presentation Laterality. Our participants were characterized by a high finger temperature when they did not attend to angry prosody presented to their right ear. CIs revealed that only angry prosody presented to the right ear that was not attended (CI: 0.0020 < NA, attention left < 0.0129) significantly differed from the NN utterances (all other CIs: -0.0033< NA, attention right < 0.0080; -0.0055

< AN, attention left < 0.0065; -0.0029< AN, attention right < 0.0074). The ANOVA for forehead temperature did not reveal any significant effect.

Discussion

Effects of Angry Versus Neutral Prosody

In the present study, participants displayed a general slowing of their responses in the sex discrimination task when they were confronted with an angry as compared with a neutral prosodic utterance. This finding is in line with the idea of increased exogenous attention toward the more survival-relevant angry prosody. It has been shown that emotional activation (e.g., evoked by emotional stimuli and emotional music) can modulate the excitability of the primary motor cortex, particularly so in the case of negative emotional reactions (Baumgartner, Willi, & Jäncke, 2007). Therefore, the longer reaction times for angry as compared with neutral prosody in our study may have been a direct consequence of such changed motor cortex activation.

The physiological data also speak to increased exogenous attention and mobilization when participants are confronted with angry as compared with neutral prosody, which was expressed in increases in mean skin conductance and forehead temperature. These results are in accordance with earlier studies on anger in which there were a variety of different experimental tasks and stimuli other than prosody. For instance, Levenson et al. (1990) reported heightened electrodermal activity, and Zajonc and collaborators (McIntosh et al., 1997; Zajoncet al., 1993) identified increased forehead temperature as specific features of negative emotions such as fear and anger.

It might be argued, however, that we cannot be sure that differences between angry and neutral prosody in our study really are a result of angry versus neutral prosody. They could, alternatively, be explained by the fact that, in the anger conditions, angry prosody was presented to only one ear while the other received neutral prosody, whereas the neutral condition consisted of neutral prosody being presented to both ears. The angry conditions, therefore, may have been characterized by higher ambiguity or conflict. Ambiguity versus emotion effects can be distinguished by the inclusion of an AA condition in future studies. Given that our results are in line with earlier studies on emotion, we nonetheless think that ambiguity cannot be held responsible for the entire effect size that we obtained for angry versus neutral prosody. For instance, if the AN and NA combinations really had only provoked greater ambiguity than the NN combinations, the Brosch et al. (2008) cross-modal study should have found a general slowing of reaction times for the dot detection in the AN and NA voice conditions in comparison with the NN condition (or no difference at all). However, that dot detection was facilitated in exactly those cases in which the dot location corresponded to the space region where the angry prosody had been presented before, speaks to the attraction of attention to angry prosody. Ambiguity in AN and NA combinations should have counteracted such an effect because one would expect attention to oscillate between left and right regions of the space. Importantly, the results discussed in the following section are unchallenged by a potential confound of ambiguity because only the supposedly ambiguous conditions AN and NA were compared.

Modulation of Responses to Angry Prosody by Varying Attention Focus and Presentation Laterality

We found a trend for a slowing of reaction times when angry prosody was unattended (Figure 1). This trend conflicts with our expectations and with the results in a previous study (Grandjean et al., 2005; Sander et al., 2005) that observed longer reaction times when angry prosody presented to the left ear was attended. The discrepancy in behavioral responses between the two studies can possibly be attributed to differences in ITIs, (approximately 9 s in the current study and 5 s in the Grandjean et al., 2005, and Sander et al., 2005 study) and needs further investigation. Because in the current study there was only a trend for the interaction Attention Focus × Presentation Laterality, we will abstain from overinterpreting this effect and the discrepancy with previous studies.

Both mean skin conductance and finger temperature responses to angry prosody varied as a function of attention focus. Higher skin conductance was observed for attended as compared with unattended angry prosody. These data conform to activity observed in the medial portion of the orbitofrontal cortex in the Sander et al. (2005) study with the same stimulus material. The authors of the latter study found higher activation in this area when angry prosody was attended than when it was not, irrespective of laterality of presentation. Such an observation strengthens, although indirectly, the idea of a strong link between skin conductance and the medial OFC, as suggested by lesion studies (Bechara, Damasio, & Damasio, 2000).

Finger temperature, in contrast to mean skin conductance, was further sensitive to laterality of presentation of angry prosody. We observed an increase in finger temperature when angry prosody was presented to the right ear, but only when this ear was outside the focus of voluntary attention. At first glance, this seems surprising, because one would expect the greatest change in finger temperature when angry prosody is in the center of attention. However, it is well possible that finger temperature changes resulting from peripheral vasodilatation in the service of fight preparation (Levenson et al., 1990) are most pronounced when something is perceived outside the focus of endogenous attention. Voluntary attention to the angry utterances may well have initiated adaptation processes in order to modify such upcoming response preparation according to existent norms. Societal behavior standards often request the suppression of aggression. Voluntary attention could thus activate control mechanisms with the goal of down-regulating and counteracting automatic response tendencies, as possibly reflected in the unattended condition. An alternative explanation could be that angry prosody, when voluntarily attended to, is perceived as more threatening, consequently changing an initial fight tendency into a withdrawal tendency in some participants. Withdrawal motivation has been associated with decreases in finger temperature (Levenson et al., 1990). Because research on the psychological significance of finger temperature is relatively sparse, each interpretation remains premature and the effect needs further investigation. However, the fact that the effect was restricted to the right ear questions the hypothesis of a general right-hemisphere advantage for the processing of angry prosody.

Heart period data also contradict the view of a general right-hemisphere advantage for the processing of angry prosody because longer heart periods were observed when angry prosody was presented to the right ear than when it was presented to the left ear. Our heart period data can thus be linked to research conducted by Harmon-Jones and collaborators (e.g., Harmon-Jones & Allen, 1998), who associate the left frontal cortex with anger and associated response tendencies. Our results for heart period are further in line with the observed left-hemisphere advantage reported by Brosch et al. (2008).

These left-lateralized effects may also be related to the linguistic structure of the pseudo-words. Indeed, the pseudo-words are linguistically structured exactly as usual semantic language but without the semantic dimension. Such linguistic structure might have induced high temporal resolution auditory processes more related to the left than to the right hemisphere (see Schirmer & Kotz, 2003, for a review). Interestingly, a left-hemisphere advantage was not irrevocably reflected in all dependent variables. Skin conductance and forehead temperature did not show laterality effects at all (cf. Ethofer, Van de Ville, et al., 2009). This is not surprising because other work on emotion has also demonstrated that different somatovisceral variables may code different components of an emotional stimulus or an emotional episode (e.g., Stemmler, Aue, & Wacker, 2007).

Similarly, earlier studies (Grandjean et al., 2005; Sander et al., 2005) revealed that some brain areas such as the amygdala and the superior temporal sulcus respond to angry prosody irrespective of voluntary attention, whereas the effect of angry prosody on activity in other areas such as the orbitofrontal cortex was modulated by focus of voluntary attention. Consistent with these observations, the physiological responses studied here were differentially sensitive to effects of angry versus neutral prosody, attentional modulations for the processing of angry prosody, and laterality of presentation of angry prosody. Forehead temperature, for instance, was sensitive to the emotional content of the pseudo-words, but was insensitive toward the attention and laterality of presentation manipulations for angry prosody. Heart period, in contrast, was sensitive to the laterality of angry prosody presentation only. Skin conductance was modulated by angry versus neutral prosody and endogenous versus exogenous attentional processes to angry prosody, and, finally, finger temperature was modulated by an interaction of endogenous versus exogenous attentional processes and laterality of presentation.

Future Directions

Our results do not allow for inferences, whether the demonstrated results are specific for angry voice prosody or whether they can also be generalized to cues associated with other emotions, particularly positive emotional prosodies. We also have no indication of whether our results in the auditory domain generalize to visual material such as facial expressions. Because of the necessity of a sufficiently high number of trials per condition, however, we were unable to test all of these questions in the current study. Future studies could address these questions by substituting neutral prosody with happy prosody or by substituting auditory with visual material. Given that sex differences have been demonstrated in previous studies on the perception of emotional prosody (e.g. Schirmeret al., 2005), it also remains to be investigated whether the effects observed in our study generalize to male participants.

Participants in our study performed a sex discrimination task and were not explicitly asked to judge emotional prosody. It is possible that the results would be different if individuals were asked to tell the type of emotional prosody presented to either the left or the right ear. Modulation of behavioral and brain responses to emotional prosody by task instructions has been investigated (e.g., Ethofer, Kreifelts, et al., 2009; Grimshaw, 1998; Kitayama & Ishii, 2002; Schirmer & Kotz, 2003). Mitchell, Elliott, Barry, Cruttenden, & Woodruff (2003), for example, demonstrated that the right middle temporal gyrus was more strongly activated when the emotional content rather than the semantic content of vocal stimuli was attended to (cf. Ethofer et al., 2006). Comparably, Bach et al. (2008) reported stronger amygdala activation during sex labeling than during emotion labeling, but stronger prefrontal and anterior cingulate activation during emotional labeling than during sex labeling. Because the amygdala can innervate the autonomic nervous system via the hypothalamus and the brainstem (e.g., LeDoux, 2000; Yang et al., 2007), changing task instructions may well be able to alternate the physiological responses that we observed in the current study. It would thus be interesting to study the influence of varying task instructions on our observed effects.

Factors such as emotional valence (Davidson et al., 1999; Rosadini & Rossi, 1967), duration, rhythm, and intensity of emotional prosody (Sidtis & Van Lancker-Sidtis, 2003; Van Lancker & Sidtis, 1992) or linguistic load (Mitchell & Ross, 2008; Ross, Thompson, & Yenkosky, 1997; Van Lancker, 1980) have further been suggested to moderate hemispheric lateralization (see Kotz, Meyer, & Paulmann, 2006, for an overview and further considerations). The systematic manipulation of these factors and the investigation of their effects on peripheral autonomic responses may be addressed in future studies.

Conclusions

Our data show differential sensitivities of the examined physiological measures for effects of angry voice prosody, voluntary attention, and laterality of presentation of angry prosody. The observed pattern of responses suggests that angry prosody attracts attention and provokes marked behavioral and physiological changes. Importantly, voluntary attention does not seem to be a prerequisite for some bodily changes (such as heart period, finger and forehead temperature) to occur, thus proposing that rudimentary analysis of the stimulus and adaptive response preparation take place even when the source of threat is outside the focus of voluntary attention. Together, our physiological data also clearly demonstrate that large parts of the concrete pattern of an effectuated mobilization may depend on the focus of voluntary attention and/or on which ear receives the prosodic threat information. Finally, our results are not supportive of the idea of a general right hemisphere-advantage for the processing of angry prosody.

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Figure Captions

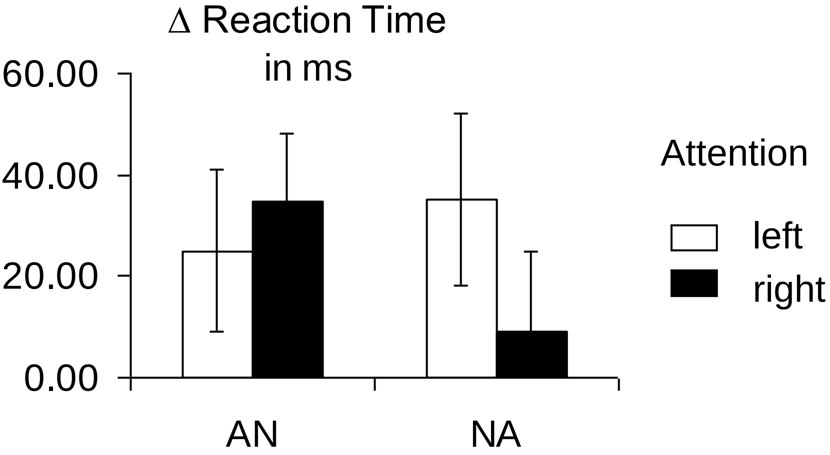
Figure 1. Reaction time as a function of attention focus and presentation laterality. Error bars depict standard errors. Reaction times for neutral (NN) prosody attended with the left (right) ear have been subtracted from reaction times for angry (AN and NA) prosody attended with the left (right) ear to reduce global sensitivity differences between the two ears.

Figure 2. Physiological changes as a function of attention focus and presentation laterality. Error bars depict standard errors. Responses to neutral (NN) prosody attended with the left (right) ear have been subtracted from responses to angry (AN and NA) prosody attended with the left (right) ear to reduce global sensitivity differences between the two ears.

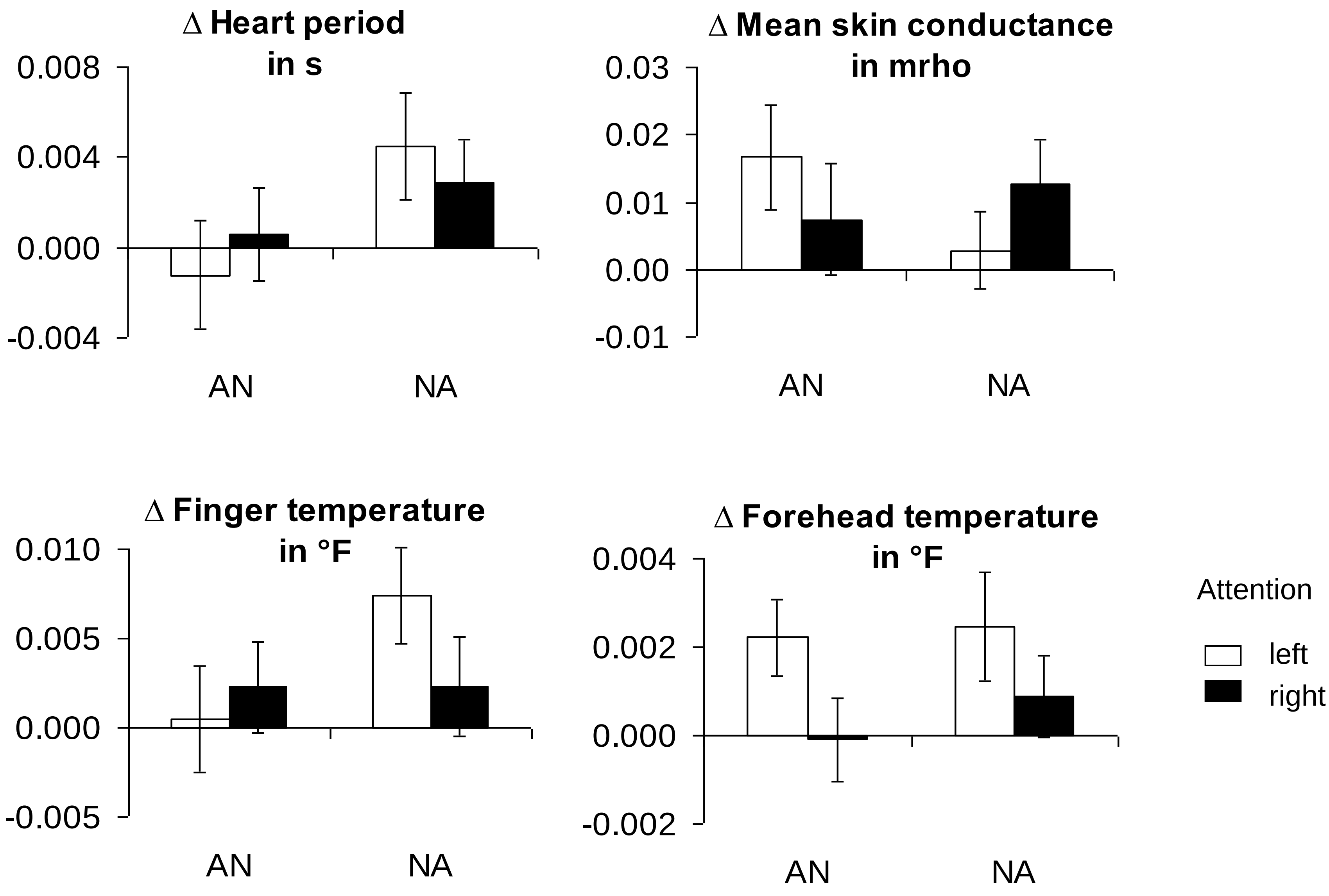
Table 1

Effects of Attention Focus (Attention) and Laterality of Presentation (Presentation) for Angry Prosody

Variable	Effect	*df*	*F*	*p*	Partial η^2
Heart period	Attention	1,40	0.00	ns	.00
	Presentation	1,40	4.68	< .05	.10
	Attention × Presentation	1,40	1.07	ns	.03
Mean skin conductance	Attention	1,41	0.00	ns	.00
	Presentation	1,41	0.54	ns	.01
	Attention × Presentation	1,41	6.73	< .05	.14
Finger temperature	Attention	1,41	0.17	ns	.00
	Presentation	1,41	3.19	.08	.07
	Attention × Presentation	1,41	5.09	< .05	.11
Forehead temperature	Attention	1,41	2.43	ns	.06
	Presentation	1,41	0.81	ns	.02
	Attention × Presentation	1,41	0.21	ns	.01



Δ Reaction Time
in ms
60.00
40.00
20.00
0.00
AN
NA
Attention
left
right



Δ Heart period
in s
0.008
0.004
0.000
-0.004
AN
NA
Δ Mean skin conductance
in mrho
0.03
0.02
0.01
0.00
-0.01
AN
NA
Δ Finger temperature
in °F
0.010
0.005
0.000
-0.005
AN
NA
Δ Forehead temperature
in °F
0.004
0.002
0.000
-0.002
AN
NA
Attention
left
right